Reprinted from American Fisheries Society Symposium, number 25, 2001, pp. 123-136. Govoni and Hare: The Charleston Gyre as a Spawning and Larval Nursery Habitat for Fishes. In: Sedberry, George R. (ed.), Island in the stream: oceanography and fisheries of the Charleston Bump. With permission from the American Fisheries Society.

American Fisheries Society Symposium 25:123–136, 2001

The Charleston Gyre as a Spawning and Larval Nursery Habitat for Fishes

JOHN J. GOVONI AND JONATHAN A. HARE
National Oceanic and Atmospheric Administration, National Ocean Service
National Centers for Coastal Ocean Science
Center for Coastal Fisheries and Habitat Research
101 Pivers Island Road, Beaufort, North Carolina 28516-9722 USA

Abstract.—The region of the outer continental shelf and upper slope, encompassed roughly by 32 and 33°N and 78 and 79°W, is unique within the southeastern Atlantic coast of the United States because of the frequent presence of large (amplitudes of 50–100 km), cyclonic eddies. These eddies develop continuously north of the deflection of the Gulf Stream at the Charleston Bump and decay downstream. The cyclonic circulation of these eddies brings nutrient-rich water from deep and off the shelf edge to near surface and results in enhanced primary production. Succession of zooplankton assemblages, driven by enhanced primary production, might serve fish production by providing an exceptional, and more continuous food supply for larval fishes spawned in or entrained into eddies. In addition, larval fishes that risk entrainment into the Gulf Stream and consequent loss from local populations, can be retained on, or near, the shelf when embedded within these eddies. The residence of an eddy within the region ranges from a week to a month or two, while the larval period of most fishes ranges from weeks to months. The large-scale eddies in the region develop most frequently in winter when the Gulf Stream is in its strongly deflected mode, coincident with the spawning of a suite of commercially important fishes. Although the region of the Charleston Gyre has the potential to act as an important spawning and nursery habitat, published evidence of usage of the habitat afforded by large scale eddies in this region is weak. High concentrations of larval fishes occasionally occur in the region, but there is no indication of high concentrations of fish eggs. With its high primary and secondary production, succession of zooplankton assemblages, and retention mechanism, the region of the Gyre may constitute an important spawning and nursery habitat for fishes, but more research aimed at assessing this potential is necessary.

The biological oceanographic literature often views the Charleston Gyre (Figure 1) as a feature that forms in the wake of the deflection of the Gulf Stream just north of the Charleston Bump, persists and remains stationary for several months, and has enhanced primary and secondary production (e.g., Atkinson and Menzel 1985; Verity et al. 1993a; Ryan and Yoder 1996). Higher primary and secondary production and potential larval retention within the Gyre might provide favorable habitat for fish spawning and for larval and juvenile growth and survival; hence, this region might well be an important contributor to fisheries production off the southeastern Atlantic coast of the United States from northern Florida to Cape Hatteras (the South Atlantic Bight [SAB] by convention, although this name has no official geographic validity). Physical data that describe the region north of the Bump indicate that the circulation and hydrographic conditions are complex. This paper seeks to evaluate the region of the Gyre as a potential spawning and fish nursery habitat in light of the physical complexity and to set forth recommendations for future research to assess the importance of the region to fish recruitment and fisheries production in the SAB.

Oceanographic Background

Physical oceanography

The Gulf Stream flows approximately parallel to the 200 m isobath in the SAB, but its course varies owing to the formation of wave-like meanders (Bane et al. 1981, and 2001, this volume). Cyclonic frontal eddies form within the offshore part of meander troughs and move northward as meanders propagate (Bane et al. 2001). Upwelling arises within the core of these eddies. The meander crest that lead a frontal eddy can interact with the eddy's cyclonic circulation and form warm filaments that wrap southward along the inshore side of the eddy. These features, a wave crest followed by a trough with cyclonic circulation that propagate northward, account for most of the sub-tidal variability in flow on the outer shelf in the SAB (Brooks and Bane 1983; Lee et al. 1991).

Two areas of diverging isobaths on the outer shelf of the SAB effect eddy growth: north of the Florida Straits and north of a topographical rise on the continental slope, the Charleston Bump (Brooks and Bane 1978; Legeckis 1979; Olson et al. 1983; Lee et al. 1991). Frontal eddies that form between the Florida Straits

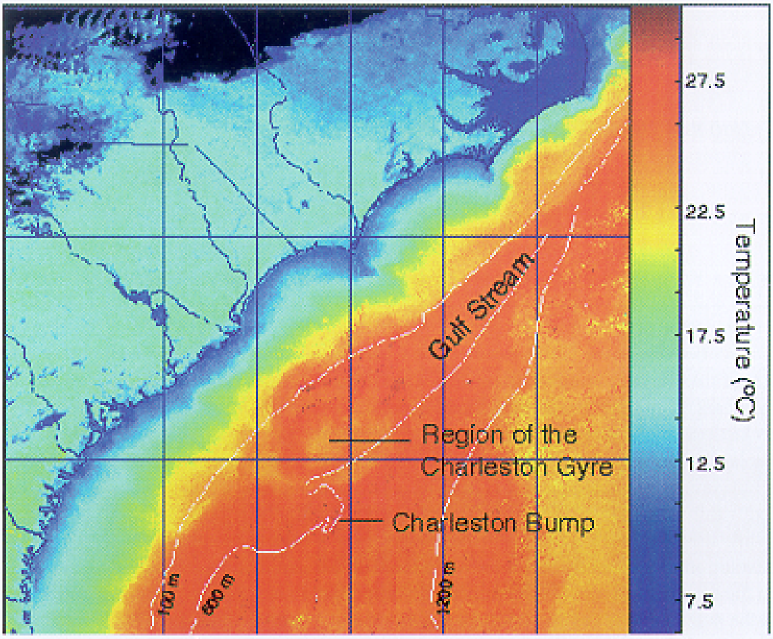


FIGURE 1. Satellite-derived, advanced, very high resolution radiometer image of sea-surface temperature showing the Gulf Stream, the topographic feature known as the Charleston Bump and the region of the Charleston Gyre. A large, well developed cyclonic eddy is evident in the region of the Charleston Gyre. This eddy's dimensions are ~160 km along-Stream and ~130 km across-Stream. Image is a 3 d composite of maximum values, 7–9 January 1999.

and the Bump have wavelengths of 100–200 km, amplitudes of 30–50 km, periods of 4–7 d, and propagation speeds of 30–50 cm s^{-1} (Lee et al. 1991). Eddy growth in the second area, just north of the Bump, is augmented by the frequent offshore displacement of the Gulf Stream by the topography of the Bump (Brooks and Bane 1978; Legeckis 1979); this results in increasing variance in the position of the Gulf Stream front (Figure 2). The Gulf Stream path in this region exhibits two states: weakly-deflected, onshore, and strongly deflected, offshore (Bane and Dewar 1988; Lee et al. 1989; Bane et al. 2001). The weakly deflected state is more common in summer, while the strongly deflected state is more common in winter (Figure 3). The offshore displacement (Hood and Bane 1983) results in the formation of large cyclonic eddies (Bane and Dewar 1988), with wavelengths of 150–300 km, amplitudes of 100 km, periods of 14–20 d, and propagation speeds of 20–50 cm s^{-1}. Downstream of the Bump, eddies decay and transfer energy back to the main current of the Gulf Stream (Lee et al. 1991), but eddies can remain intact past Cape Fear and even Cape Hatteras (Glenn and Ebbesmeyer 1994).

Satellite-derived images of sea-surface temperature (SST) often show a large eddy associated with the offshore deflection of the Gulf Stream just north of the Charleston Bump (Figure 1). Warmer water that projects southwards along the inshore edge indicates cyclonic circulation. Domed isotherms, indicative of upwelling, are commonly observed here as well (Figure 4). Such observations have given rise to the term the Charleston Gyre (Bane 1983; Singer et al. 1983): a meso-scale, stationary, cyclonic eddy that can persistent for months in the wake of the Bump (Verity et al. 1993a; Ryan and Yoder 1996).

The processes that lead to meso-scale eddy formation just north of the Charleston Bump are continuous, especially when the Gulf Stream is in the strongly deflected state. As eddies form and often propagate northeastward, eddy formation just north of the Gulf Stream deflection continues. Rather than one eddy that lingers over the slope for months, current-meter records and serial images of SST indicate multiple, large amplitude, propagating eddies. For example, current measurements on the South Carolina outer shelf indicate that a series of meso-scale eddies moved along the shelf break during the winters of 1981–1982 and 1985–1986 (Bane and

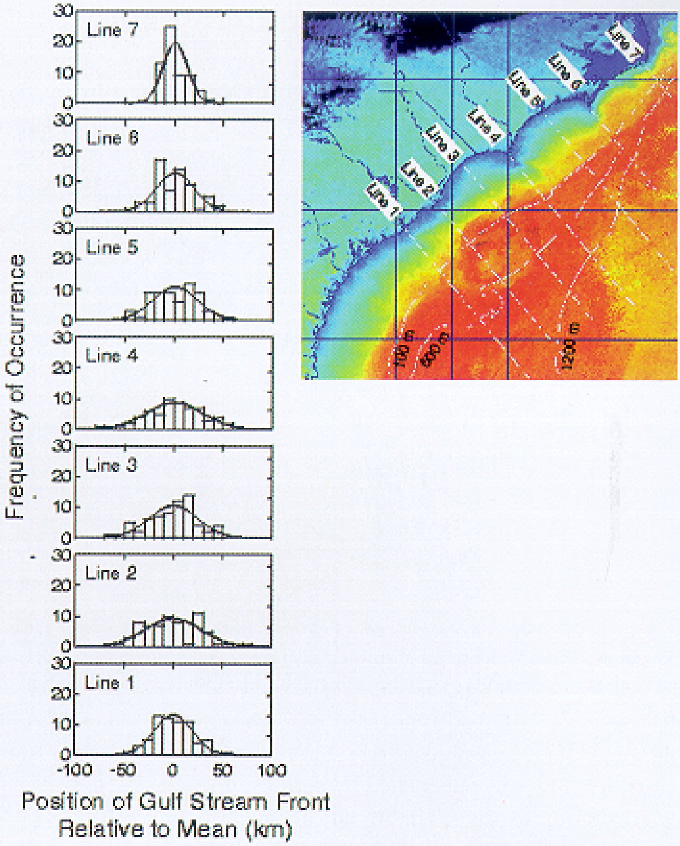


FIGURE 2. Deviations in the Gulf Stream frontal locations relative to the mean position along seven transects from Charleston, South Carolina to Cape Hatteras, North Carolina. Data derived from 3 d maximum value composite of sea-surface temperature images from 1 October 1998 to 15 April 1999.

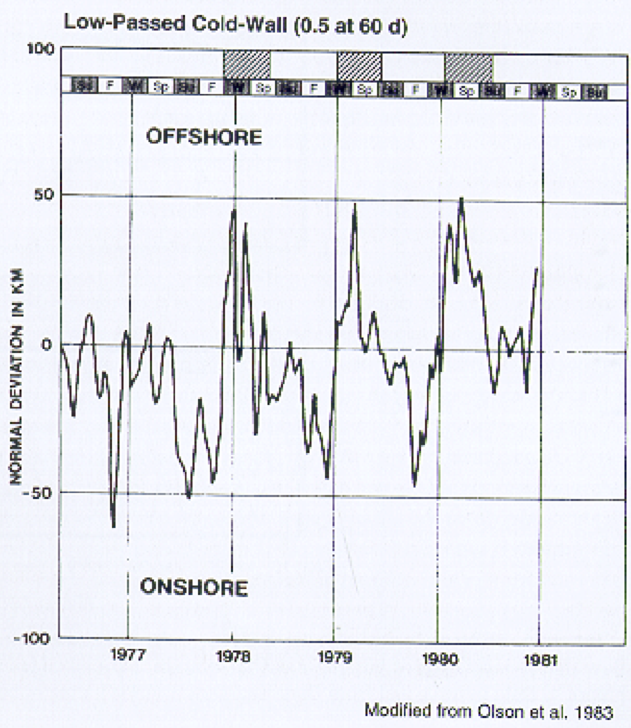


FIGURE 3. Deviations in Gulf frontal locations relative to the mean position off of Cape Fear, North Carolina over a 4.5 year period from Olson et al. (1983). Data extracted from a transect approximately equivalent to transect line 4 in Figure 2. Weekly frontal locations were low-passed filtered with a half power point at 60 d. Shaded bars along the top indicate periods when the Gulf Stream was in the strongly deflected (offshore) state. Seasons are also indicated (modified from Olson et al. 1983).

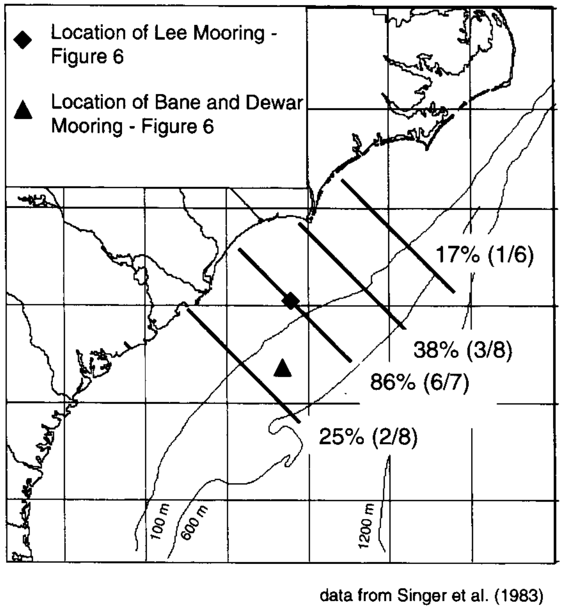


FIGURE 4. Percent observation of domed isotherms along four cross-shelf transects off the Carolinas (data from Singer et al. 1983). Number of transects sampled and number of positive occurrences of domed isothermes provided in parentheses. Locations of current meters used in Figure 5 are also shown.

Dewar 1988; Lee et al. 1989). At a fixed location on the outer shelf and upper slope, the typical northeastward flow was punctuated by periods of southward motion as the Gulf Stream meandered and cyclonic eddies propagated through the region (Figure 5). Large eddies were also seen north of the Bump from 9 to 30 October 1998, but these eddies formed and propagated northward with another eddy forming behind (Figure 6). A time-series of SST data indicate several periods of large offshore displace-

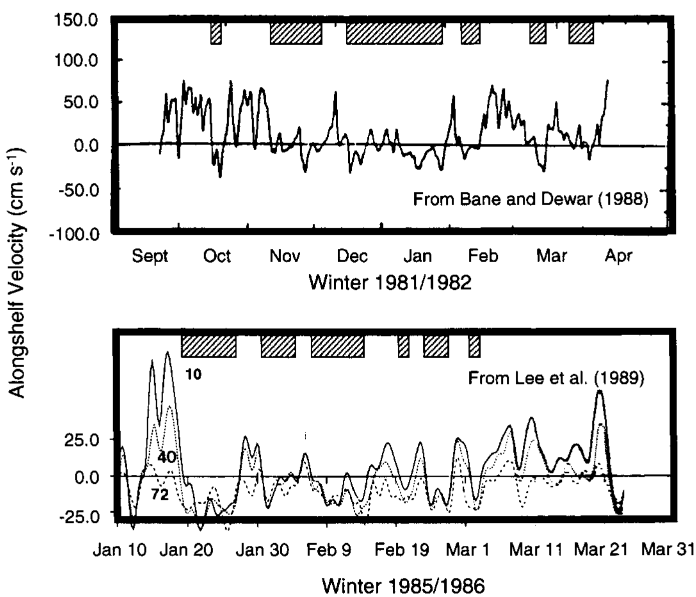


FIGURE 5. Current meter records from the outer Carolina shelf. Shaded bars highlight periods of southwestward flow that is indicative of passing meander troughs and embedded cyclonic circulation. Mooring locations shown in Figure 4. Data in top panel from Bane and Dewar (1988); data in bottom panel from Lee et al. (1989).

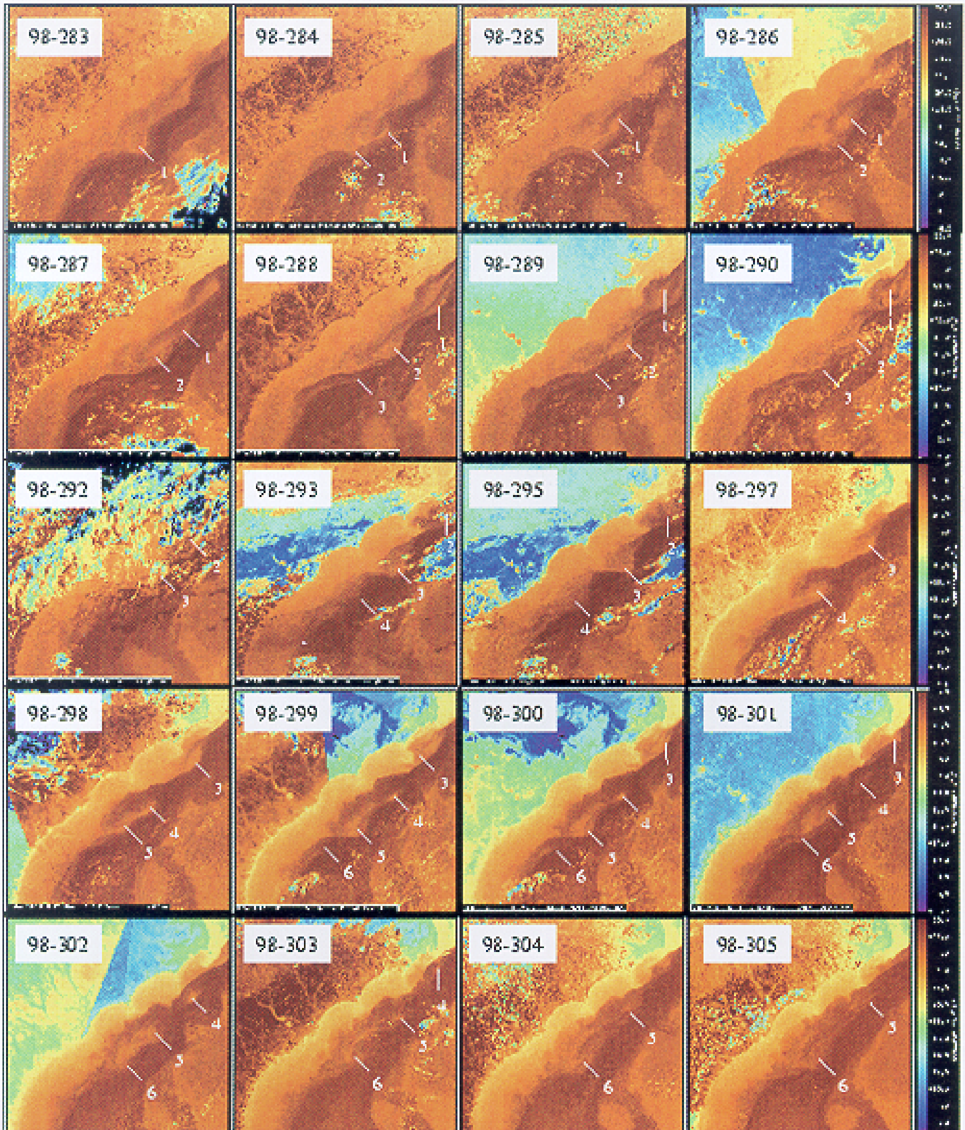


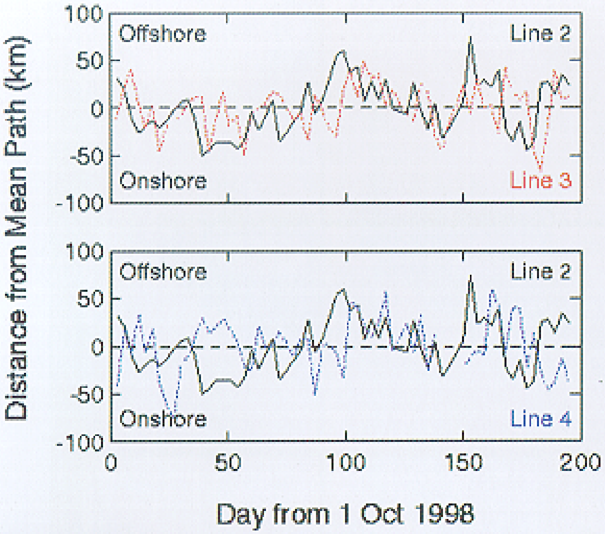
FIGURE 6. Serial SST images for the region of the Charleston Gyre. Three day maximum value composite sea-surface temperature images from 9 to 30 October 1998 is shown. White numbers signify individual eddies as they propagate northwards over time. Numbers in upper left corner of each panel identifies year and day of the year of each image.

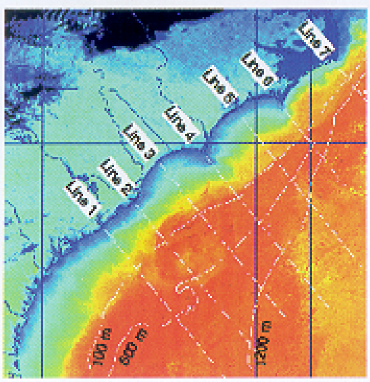
ment in the Gulf Stream front that propagate downstream (Figure 7).

The region characterized by the feature commonly known as Charleston Gyre is unique within the SAB, because of its semipersistent, cyclonic, meso-scale circulation. Physical oceanographic observations indicate the persistent occurrence of large cyclonic eddies north of the Bump (Figure 1). Rather than simply a stationary feature, multiple eddies form and propagate through the region (Figure 7). At issue for the biology of the region is the fate of water within these eddies; that is, the Lagrangian fate of individual eddies, not simply the persistent and stationary process of eddy formation north of the Charleston Bump.

Biological oceanography

Production within the SAB differs from other warm-temperate areas of the world ocean (Table 1). As a





Transect	r^2	Lag
Line 1 v 2	0.72	-3 d
Line 2 v 3	0.59	+3 d
Line 2 v 4	0.46	+9 d
Line 2 v 5	0.33	+15 d
Line 2 v 6	ns	-
Line 2 v 7	ns	-

FIGURE 7. Cross-correlations in Gulf Stream frontal locations between transects lines identified in Figure 2. Data from transect line 2 is shown in black (just north of the Charleston Bump). Data for transect line 3 and line 4 are shown in red and blue. Table shows highest significant cross-correlation coefficients between time series of frontal locations between transect line 2 and other transect lines. Corresponding lag is also provided. Data derived from 3 d maximum value composite sea-surface temperature images from 1 October 1998 to 15 April 1999.

whole, primary production here does not vary greatly from season to season (Yoder 1985). On the inner shelf, primary production is controlled by the input of nutrients from rivers and estuaries (see reviews in Atkinson 1985; Verity et al. 1993a). Over the mid- and outer shelf, primary production is controlled by nutrients upwelled within cyclonic eddies from within or below the thermocline beneath the Gulf Stream (Verity et al. 1993a). In the winter, upwelled water often reaches near surface because shelf water is largely unstratified, but high primary production that results from this nutrient flux is constrained to the outer shelf because vertical isopycnals that define the outer shelf front block the shoreward projection of upwelled water (Pietrafesa et al. 1985; Lee et al. 1991; Ryan and Yoder 1996). In summer upwelled water typically intrudes shoreward near the bottom, under the stratified water column of the shelf (Verity et al. 1993a.). Near-bottom upwelling and projection on the shelf is occasionally evident in winter (e.g., Pietrafesa 1989; Govoni and Pietrafesa 1994; Govoni and Spach 1999).

TABLE 1. Estimates of primary productivity and fishery yield in the world ocean excluding estuaries.

Ecosystem	Primary productivity (g C/ m²/year)	Fishery yield (kg/ha/year)
World ocean, continental shelf	100–400[a]	21–150[a]
World ocean, upwelling zones	60–300[a]	6–200[a]
Open ocean and coral reefs	20–250[a]	2–55[a]
Southeastern U.S., outer shelf	260[b]–360[c]	55[d]

[a] Nixon (1988); [b] Lee et al. (1991); [c] Verity et al. (1993a); [d] Marten and Polovina (1982).

The region of the Charleston Gyre exhibits high primary productivity relative to other areas of the SAB (Lee et al. 1991). Lee et al. (1991) indicated net on-shelf nutrient flux and net carbon fixation in two regions of the SAB, both north of the two recognized regions of eddy formation. Ryan and Yoder (1996) show distinct phytoplankton pigment fields adjoining the region and exceptionally high concentrations of chlorophyll in the region, but they also found more frequent and similarly high concentrations of chlorophyll along the mid-shelf front. Satellite-derived images of sea-surface color show high chlorophyll concentrations in large cyclonic eddies in the region, but these chlorophyll features can propagate northward with the SST signature of these eddies (Figure 8).

The high episodic primary production induced by Gulf Stream meanders and intrusions induces intermittently high secondary production, that is, high zooplankton abundance, on the mid- and outer shelf (Paffenhöfer 1985; Verity et al. 1993a, 1993b). While there are no composite estimates of secondary production in units of carbon fixation or energy transfer, the abundance of single taxa of zooplankton in the SAB approaches the high levels characteristic of the major upwelling zones and fishing areas of the global ocean such as the Peruvian upwelling zone and off the Ivory Coast of Africa and Oregon, USA (Paffenhöfer 1985).

The region of the Charleston Gyre provides an area of persistently high primary and secondary production where parcels of water contain assemblages of zooplankton that succeed in size and taxonomic constitution. The magnitude of zooplankton abundance and the maturity of the succession depends on the residence time of upwelled, nutrient rich water. Salps and doliolids, that are injected from the Gulf Stream and that reproduce asexually, increase in abundance first (Verity et al. 1993a, 1993b). The mucous-nets of these zooplankters enable feeding on bacteria that are stimulated in growth by phytoplankton exudates. Aloricate protozoans, also bacteria-feeders, are also abundant on the outer shelf in the SAB (Verity et al. 1988), and may be stimulated in growth by bacterial abundance in upwelled water. Cyclopoid and small calanoid copepods, along with cladocerans and larvaceans follow. As upwelled water propagates and ages, older upwelled water contains mostly larger calanoid copepods (Paffenhöfer 1985).

Fishery oceanography

The fisheries of the SAB have attributes of warm temperate and semitropical areas, with production and harvest of warm temperate (principally clupeid, sciaenid, paralichthyid), reef (serranid, lutjanid, and sparid), coastal pelagic (scombrid), and highly migratory (thunnine scombrid, istiophorid, and xiphiid) fishes. At 5.5 metric tons km^{-1} year^{-1} on the shelf (out to the 110 m isobath), fishery production in the SAB is lower than the major upwelling zones of the world, but is higher than the waters over most continental shelves of warm-temperate and tropical oceans (Table 1).

Two fisheries have recently emerged in the vicinity of the Charleston Bump and in the region of

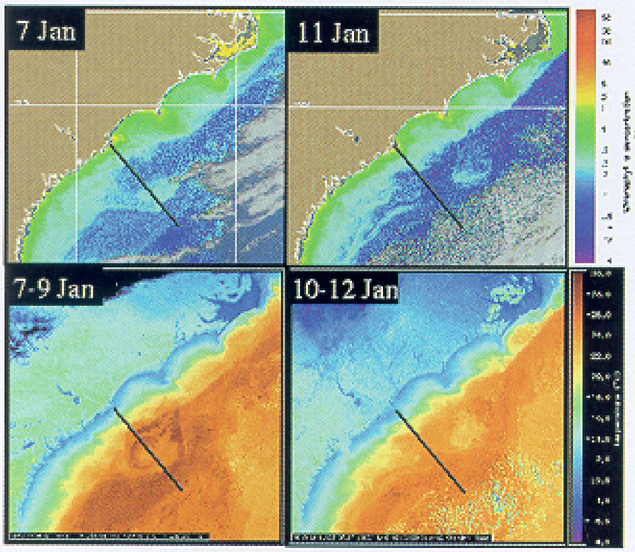


FIGURE 8. Comparison of estimates of sea-surface chlorophyll-a concentration and sea-surface temperature for two days during January 1999. Chlorophyll-a concentrations derived from visual band data from SeaWIFS satellite and processed using R. Stumpf's chlorophyll algorithm (NOAA, National Ocean Service, Silver Spring, Maryland). Line provided across images to infer relative position of cyclonic eddy between images.

the Charleston Gyre that have added to these production estimates. An active fishery for wreckfish *Polyprion americanus* began in the late 1980s over the Bump (Vaughan et al. 2001, this volume). Large longline catches of the highly migratory fish, swordfish *Xiphias gladius*, became common within the region in the 1980s (Cramer 1996).

Concentrations of larval fishes, fishery-independent indicators of fishery production, vary in the SAB. Variation is greater across the shelf than it is along the shelf (Yoder 1983). In the winter, when many fishes of commercial importance spawn in the offshore waters of the SAB (principally the estuarine dependents including Atlantic menhaden *Brevoortia tyrannus*, spot *Leiostomus xanthurus* and Atlantic croaker *Micropogonias undulatus*, and paralichthyd flounders), larval fishes are often densely distributed over the outer shelf, with concentrations that exceed five larvae m^{-3} (Paffenhöfer 1985; Govoni 1993). In summer, when many reef, coastal pelagic, and migratory fishes spawn, larvae are more evenly distributed and concentrations are considerably lower (Yoder 1983; Govoni 1993; Powell and Robbins 1994, 1998).

High concentrations of larval fishes do not translate to exceptionally high fishery production (Table 1). Within an ecosystem, primary and secondary production contribute the energy that fuels the growth and survival of larval and juvenile fishes and drives recruitment to adult populations. Larval, juvenile, and adult fishes grow faster when and where food is abundant, yet the linkage of primary and fishery production is not always tight (e.g., Nixon 1988). Ratios of fish yield to primary production range from the order of 10^{-6} in the open ocean, through 10^{-5} over continental shelves, to 10^{-4} coastal upwelling zones (Marten and Polovina 1982). A most plausible explanation for the loose correlation of primary and fishery production (Nixon 1988) is that the intermediate connection, secondary production, is complex (e.g., Mann 1993; Cushing 1995); hence, the concept of food webs versus food chains (e.g., Legendre and Rassoulzadegan 1995). Each additional linkage carries a reduction of energy transfer of about 50% (Mann 1993). For larval and adult fishes the complexity and resulting reduction in transfer efficiency can be considerable (e.g., Nielsen and Richardson 1996).

Whereas there is substantial evidence that growth rates of larval fishes are positively correlated with survival (Meekan and Fortier 1996; Hare and Cowen 1997), evidence for the correlation of growth and the recruitment of juveniles to populations is equivocal. A possible explanation is that factors other than food supply, principally predation (Bailey and Houde 1989) and the inimical results of physical transport (Hare and Cowen 1996; Govoni and Spach 1999; Cowen et al. 2000), compromise recruitment. An alternative explanation is that those factors that are conducive to the growth and survival of larvae may not be conducive to the survival of juveniles (Bertram and Leggett 1994; Hare and Cowen 1997; Buckel et al. 1998).

Paffenhöfer (1985) suggested that the episodic nature of eddies, upwelling, and resultant primary and secondary production, as well as the loss of larval fishes by entrainment into the Gulf Stream, limits the translation of primary production to fishery production in the SAB. The region of the Charleston Gyre, however, is an area of persistent upwelling, high primary and secondary production, and cyclonic circulation where larval fishes might feed and be retained. This region may well be a critical habitat for the spawning, retention, and survival of larvae in the SAB, but this is neither understood nor established.

Potential of the Region of the Charleston Gyre as Spawning and Nursery Habitat of Fishes

The following questions should be addressed to assess the potential of the region of the Charleston Gyre as an important spawning and nursery habitat within the SAB: (1) Are adult fishes more abundant in the region and is spawning evident there, that is, are there spawning aggregations or high abundance of fish eggs there?; (2) Are larval fishes more abundant in the region than elsewhere in the SAB?; (3) Are larval fishes retained by advective processes in the region?; (4) Is the persistent secondary production that is characteristic of the region available to and consumed by larval fishes?; (5) What is the abundance of larval fish predators in the region and do they consume larval fishes?

Spawning aggregations and the distribution of adult fishes and fish eggs in the region of the Charleston Gyre

Evidence of spawning aggregations within the region of the Charleston Gyre is weak. The prevalence, that is, presence or absence, of demersal and pelagic fishes in otter trawl catches taken in spring, summer, fall, and winter from 1973 to 1975, was no greater within the region (here arbitrarily encompassed by 32 and 33°N and 077–079°W), than it was elsewhere over the outer shelf of the SAB (Wenner et al. 1979a, b, c, d, 1980). Atkinson and Targett (1983) recorded aggregations of acoustic echo returns that coincided with upwelling within the region, but they did not verify targets as fishes. Whether fishes focus their spawning within the Gyre remains a question, largely because surveys of adult fishes in the SAB have been intermittent and of coarse spatial scale. Rarely have fish eggs been systematically identified and counted in the SAB; those of Atlantic menhaden constitute the sole exception. Eggs are widely distributed over the outer shelf (Judy and Lewis 1983; Checkley et al. 1999).

The abundance and distribution of fish larvae in the region of the Charleston Gyre

While the diversity of larval fishes is higher within the region of the Charleston Gyre than it is elsewhere in the SAB (Fahay 1975), this high diversity probably owes to the exchange and mixing of Gulf Stream and shelf water and the different assemblages of fishes that these water masses contain. The larvae of semitropical, tropical, and highly migratory fishes traveling northward in the Gulf Stream mix with the larvae of warm-temperate fishes on the shelf (Powell and Robins 1994, 1998; Govoni and Spach 1999). Reciprocally, a large number of larvae spawned in the SAB may be lost to local populations through entrainment into the Gulf Stream and northward transport (Hare and Cowen 1991; Govoni and Spach 1999).

Evidence of exceptional abundance of fish larvae in the region of the Charleston Gyre is weak. Powles and Stender (1976) recorded irregularly high concentrations of larval fishes (>100 beneath m^{-2} of sea-surface) over the region (again encompassed by 32 and 33°N and 077–079°W), but such concentrations also occur occasionally elsewhere in the SAB. Occasional high concentrations of larval Atlantic menhaden in winter occur within the region of the Gyre, but are also sporadically evident elsewhere in the SAB (Figure 9). High concentrations of larval bluefish *Pomatomus saltatrix* occur in the region in the autumn (Kendall and Walford 1979). Collins and Stender (1987) suggested that the region may serve as a spawning area for king mackerel *Scomberomorus cavalla*, because of the recurrent collection of small (≤4 mm) larvae there.

The frequent collection of the larvae of the highly migratory swordfish within the region of the Charleston Gyre indicates that the region might be a nursery area, but not a principal spawning area, for that species. The collection of smallest and youngest larvae along the western edge of the Gulf Loop Current indicates that spawning is probably focused in the eastern

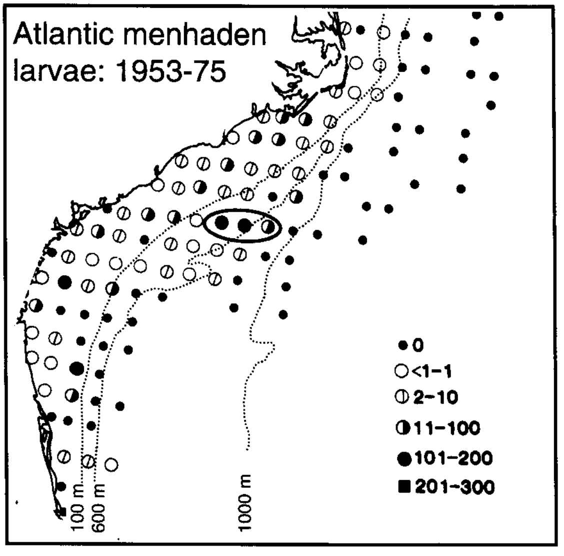


FIGURE 9. The mean abundance and distribution of Atlantic menhaden *Brevoortia tyrannus* larvae in off the southeastern Atlantic coast of the United States, January to March 1953–1975. High mean concentrations (number of larvae m^{-3}) in the region of the Charleston Gyre are encircled (modified from Judy and Lewis 1983).

Gulf of Mexico, though marginal spawning occurs in the SAB as far north as Onslow Bay, North Carolina (Govoni et al. 2000). Five of 27 collections taken between the Straits of Florida and Cape Hatteras from 1973 and 1980 coincided with the large semipermanent cyclonic circulation that is characteristic of this region (Govoni et al. 2000). Upwelling and recirculation were clearly evident in the region in September 1988 when 11 larvae were taken along the Gulf Stream front, compared with one larva taken outside of the region. Swordfish larvae accumulate in the Gulf Stream frontal zone, and because of the frequent convolution of the Gulf Stream front within the region of the Gyre, the resolution of a relation between larval distribution and the Gyre, or a relation between larval distribution and the Gulf Stream frontal zone, will prove difficult. The recent collection of five swordfish larvae about a large, cyclonic eddy in the region of the Gyre illustrates this point (Figure 10). One larva was collected in the Gulf Stream front just south of a large cyclonic eddy on 16 January 2000. This eddy moved and stretched northeastward through 22 January, while four more larvae were collected on 18 January in what probably was then the Gulf Stream front just north of the eddy. Additional corroboration of this apparent lack of affinity of the larvae of highly migratory fishes for the Gyre proper is the occasional collection of bluefin tuna *Thunnus thynnus* in the region, but not within the Gyre (McGowan and Richards 1989).

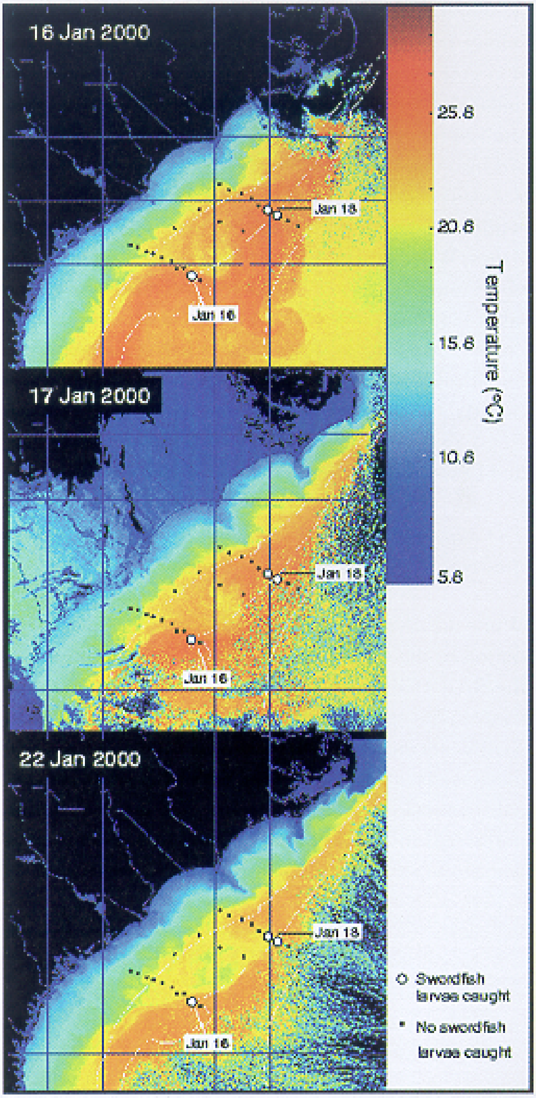


FIGURE 10. Neuston collections (black circles) in the region of the Charleston Gyre and collections that yielded swordfish *Xiphias gladius* larvae or juveniles (white circles) in January 2000. On 16 January, swordfish larvae were collected in the Gulf Stream frontal zone just south of a mesoscale cyclonic eddy. This eddy moved northeastward by 17 January and had stretched to the northeast by 22 January; swordfish larvae were collected along the northern edge of this eddy (northern most transect) in the Gulf Stream frontal zone on 18 January 2000.

The retention of larval fishes in the region of the Charleston Gyre

The loss of larval fishes to the Gulf Stream may be limited by cyclonic circulation in the region of the Charleston Gyre. Larvae hatched from eggs spawned within the region, may be entrained by the circulation of the region. Once within a propagating meso-scale eddy, eggs or larvae would circuit the eddy, perhaps several times before the eddy decayed. Residence of an eddy within the region, ranges from a week to a month or two (Figures 7 and 8; Bane and Dewar 1988; Lee et al. 1991), a span in line with typical durations of the larval period that range from weeks to months (e.g., Victor 1986; Wellington and Victor 1989; Lindeman et al. 2000). Fish larvae entrained in the cyclonic circulation of an eddy in the region will be at or near metamorphosis and could settle from the plankton before the eddy decays or propagates north of the region if appropriate settlement habitat is available on the slope or outer shelf. If adequate habitat for settlement is not available on the outer shelf, cross-shelf transport from the location of release (from an eddy) to appropriate juvenile habitats on the mid- and inner shelf (or to estuaries) is required.

Secondary production and the availability and consumption of food for larval fishes in the region of the Charleston Gyre

The succession of zooplankton assemblages within eddies apparently proceeds through taxa that are the required food of growing larval fishes. Young larvae eat primarily copepod nauplii and small copepodites, along with a variety of other small plankters including pteropods, pelecypod veligers, and tintinnids (Turner 1984), and they eat selectively with demonstrable species-specific differences in selection (Govoni et al. 1986). The copepod taxa that increase in abundance secondarily, after salps and doliolids (Paffenhöfer 1985), are of the same genera that are commonly eaten by young larval fishes: the calanoids *Paracalanus*, and the cyclopoids *Temora*, *Oithona*, and *Oncaea* (Govoni et al. 1983). Further, young larvae might rely more heavily on aloricate protozoans or other products of the microbial food web than previously recognized (Fukami et al. 1999). The microbial food web itself is not well understood in the SAB (Pomeroy 1985), while the linkage of this trophic loop to fishery production remains largely unexplored (Cushing 1995). Older upwelled water contains mostly larger calanoid copepods, including *Eucalanus* and *Centropages* (Paffenhöfer 1985), that are selected by older larval and pelagic juvenile fishes (Govoni et al. 1986). With regard to food supply, the region of the Charleston Gyre probably offers an excellent habitat for developing fishes.

The abundance of larval fish predators in the region of the Charleston Gyre

Beyond the predatory action of chaetognaths in Onslow Bay (Baier and Purcell 1997), little is known of the abundance and distribution of the predators of larval fishes (see review in Bailey and Houde 1989) in the SAB; nothing within the eddies that characterize the region of the Charleston Gyre.

Recommendations for Future Research

An understanding of the linkage of primary and secondary production to recruitment and fishery production in the SAB should be predicated upon an assessment of the region of the Charleston Gyre as a critical habitat for fishery production, because of the semipersistence of high primary and secondary production and recirculation in the region. Future fisheries oceanographic research should focus on examining the spatial distribution and trophic ecology of larval fishes of this region. This should be done with oceanographic field work aimed at documenting the nutrient flux, primary production, secondary production, trophic ecology of larval and juvenile fishes, and their growth histories all within the developing, propagating, and decaying eddies within the region.

Specifically, to address the first three questions—the spatial distribution of spawning, and the distribution and retention of larval fishes—the distribution of fish eggs, larvae, and juveniles should be resolved at spatial scales that are relevant to the dimensions and trajectories of the cyclonic eddies that transit the region. The resolution of larval fish advection, diffusion and survival requires the coupling of Lagrangian and Eulerian measurements of flow fields. The distributions resolved from a scale that encompass the region of the Gyre must be compared with distributions at a scale that encompasses the entire SAB.

To address the last two questions—the availability and usage of the products of secondary production, the age and growth of larval and juvenile fishes, and the predator field—the trophic interactions of larvae and juveniles, including predation upon larvae and juveniles, should be described and quantified within the context of eddy growth and decay, and plankton succession.

Acknowledgments

We thank J. M. Bane who commented on the interpretation of the physical dynamics of the Charleston Gyre, M. Sorraco and H. Gu who processed SeaWIFS data, and R. Stumpf, who provided the algorithm for the conversion of sea-surface color to chlorophyll concentration. National Oceanic and Atmospheric Administration, Southeast CoastWatch Program at Beaufort, North Carolina, provided satellite images. Drafts of the manuscript were reviewed by L. R. Settle, P. T. Tester, and W. J. Richards.

References

Atkinson, L. P. 1985. Hydrography and nutrients of the southeastern U.S. continental shelf. Pages 77–992 *in* Atkinson et al. (1985).

Atkinson, L. P., D. W. Menzel, and K. A. Bush, editors. 1985. Oceanography of the southeastern U.S. continental shelf. American Geophysical Union, Washington, D.C.

Atkinson, L. P., and T. E. Targett. 1983. Upwelling along the 60m isobath from Cape Canaveral to Cape Hatteras and its relationship to fish distribution. Deep-Sea Research 30:221–226.

Atkinson, L. P., and D. W. Menzel. 1985. Introduction: oceanography of the southeast United States continental shelf. Pages 1–9 *in* Atkinson et al. (1985).

Baier, C. T., and J. E. Purcell. 1997. Trophic interactions of chaetognaths, larval fish, and zooplankton in the south Atlantic bight. Marine Ecology Progress Series 146:43–53.

Bailey, K. M., and E. D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Advances in Marine Biology 25:1–83.

Bane, J. M. 1983. Initial observations of the subsurface and short-term variability of the seaward deflection of the Gulf Stream off Charleston, South Carolina. Journal of Geophysical Research 88:4673–4684.

Bane, J. M., D. A. Brooks, and K. R. Lorenson. 1981. Synoptic observations of the three-dimensional structure and propagation of Gulf Stream meanders along the Carolina continental margin. Journal of Geophysical Research 86:6411–6425.

Bane, J. M., and W. K. Dewar. 1988. Gulf Stream bimodality and variability downstream of the Charleston Bump. Journal of Geophysical Research 93:6695–6710.

Bane, J. M., L. P. Atkinson, and D. A. Brooks. 2001. Gulf Stream physical oceanography at the Charleston Bump: deflection, biomodality, meanders, and upwelling. Pages 25–36 *in* G. Sedberry, editor. Island in the stream: oceanography and fisheries of the Charleston Bump. American Fisheries Society, Symposium 25, Bethesda, Maryland.

Bertram, D. F., and W. C. Leggett. 1994. Predation risk during the early life history periods of fishes: separating the effects of size and age. Marine Ecology Progress Series 109:105–114.

Brooks, D. A., and J. M. Bane. 1978. Gulf Stream deflection by a bottom feature off Charleston, South Carolina. Science 201:1225–1226.

Brooks, D. A., and J. M. Bane. 1983. Gulf Stream meanders off North Carolina during winter and summer 1979. Journal of Geophysical Research 88:4633–4650.

Buckel, J. A., B. H. Letcher, and D. O. Conover. 1998. Effects of a delayed onset of piscivory on the size of age-0 bluefish. Transactions of the American Fisheries Society 127:576–587.

Checkley, D. M., P. B. Ortner, F. E. Werner, L. R. Settle, and S. R. Cummings. 1999. Spawning habitat of the Atlantic menhaden in Onslow Bay, North Carolina. Fisheries Oceanography 8 (Supplement 2):22–36.

Collins, M. R., and B. W. Stender. 1987. Larval king mackerel (*Scomberomorus cavalla*), spanish mackerel (*S. maculatus*), and bluefish (*Pomatomus saltatrix*) off the southeast coast of the United States, 1973-1980. Bulletin of Marine Science 41:822–834.

Cowen, R. K., K. M. M. Lwiza, S. Sponaugle, C. B. Paris, and D. B. Olson. 2000. Connectivity of marine populations: open or closed? Science 287:857–859.

Cramer, J. 1996. Recent trends in the catch of undersized swordfish by the U.S. pelagic longline fishery. Marine Fisheries Review 58(3):24–32.

Cushing, D. 1995. Population production and regulation in the sea, a fisheries perspective. Cambridge University Press, Cambridge, UK.

Fahay, M. P. 1975. An annotated list of larval and juvenile fishes captured with surface-towed meter net in the south Atlantic bight during four RV Dolphin cruises between May 1967 and February 1968. NOAA (National Oceanic and Atmospheric Administration) Technical Report. NMFS (National Marine Fisheries Service) SSRF-685, Washington, D.C.

Fukami, K., A. Watanabe, S. Fujita, K. Yamaoka, and T. Nishijima. 1999. Predation on naked protozoan microzooplankton by fish larvae. Marine Ecology Progress Series 185:285–291.

Glenn, S. M., and C. C. Ebbesmeyer. 1994. Observations of Gulf Stream frontal eddies in the vicinity of Cape Hatteras. Journal of Geophysical Research 99:5047–5055.

Govoni, J. J. 1993. Flux of larval fishes across frontal boundaries: examples from the Mississippi River plume and the western Gulf Stream front in winter. Bulletin of Marine Science 53:538–566.

Govoni, J. J., D. E. Hoss, and A. J. Chester. 1983. Comparative feeding of larval fishes in the northern Gulf of Mexico: *Brevoortia patronus, Leiostomus xanthurus*, and *Micropogonias undulatus*. Marine Ecology Progress Series 13:189–199.

Govoni, J. J., P. B. Ortner, F. Al-Yamani, and L. C. Hill. 1986. Selective feeding of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropgonias undulatus* larvae in the northern Gulf of Mexico. Marine Ecology Progress Series 28:175–183.

Govoni, J. J., and L. J. Pietrafesa. 1994. Eulerian views of layered water currents, vertical distribution of some larval fishes, and inferred advective transport over the continental shelf off North Carolina, USA, in winter. Fisheries Oceanography 3:120–132.

Govoni, J. J., and H. L. Spach. 1999. Exchange and flux of larval fishes across the western Gulf Stream front south of Cape Hatteras, USA, in winter. Fisheries Oceanography 8 (Supplement 2):77–92.

Govoni, J. J., B. W. Stender, and O. Pashuk. 2000. Distribution of larval swordfish, *Xiphias gladius*, and probable spawning off the southeastern United States. U.S. National Marine Fisheries Service Fishery Bulletin 98:64–74.

Hare, J. A., and R. K. Cowen. 1991. Expatriation of *Xyrichtys novacula* (Pisces: Labridae) larvae: evidence of rapid cross-slope exchange. Journal of Marine Research 49:801–823.

Hare, J. A., and R. K. Cowen. 1996. Transport mechanisms of larval and juvenile bluefish, *Pomatomus* *saltatrix*, from South Atlantic Bight spawning ground to Middle Atlantic Bight nursery habitats. Limnology and Oceanography 41:1264-1280.

Hare, J. A., and R. K. Cowen. 1997. Size, growth, development and survival of marine planktonic larvae of *Pomatomus saltatrix*. Ecology 78:2415–2431.

Hood, C. A., and J. M. Bane. 1983. Subsurface energetics of the Gulf Stream cyclonic frontal zone off Onslow Bay, North Carolina. Journal of Geophysical Research 88:4651–4662.

Judy, M. H., and R. M. Lewis. 1983. Distribution of eggs and larvae of Atlantic menhaden, *Brevoortia tyrannus*, along the Atlantic coast of the United States. NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) SSRF-774, Washington, D.C.

Kendall, A. W., Jr., and L. A. Walford. 1979. Sources and distributions of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. U.S. National Marine Fisheries Service Fishery Bulletin 77:213–227.

Lee, T. N., E. Williams, J. Wang, and R. Evans. 1989. Response of South Carolina continental shelf waters to wind and Gulf Stream forcing during winter of 1986. Journal of Geophysical Research 94:10715–10754.

Lee, T. N., J. A. Yoder, and L. P. Atkinson. 1991. Gulf Stream frontal eddy influence on productivity of the southeast U.S. continental shelf. Journal of Geophysical Research 96:22,191–22,205.

Legeckis, R. 1979. Satellite observations of the influence of bottom topography on the seaward deflection of the Gulf Stream off Charleston, South Carolina. Journal of Physical Oceanography 9:483–497.

Legendre, L., and F. Rassoulzadegan. 1995. Plankton and nutrient dynamics in marine waters. Ophelia 41:153–172.

Lindeman, K. C., R. Pugliese, G. T. Waugh, and J. S. Ault. 2000. Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats, and protected areas. Bulletin of Marine Science 66:929–956.

Mann, K. H. 1993. Physical oceanography, food chains, and fish stocks: a review. ICES Journal of Marine Science 50:105–119.

Marten, G. G., and J. J. Polovina. 1982. A comparative study of fish yields from various tropical ecosystems. Pages 255–289 *in* D. Pauly and G. I. Murphy, editors. Theory and management of tropical fisheries. ICLARM (International Center for Living Aquatic Resources Management) Conference Proceedings 9. ICLARM, Manila, Philippines and Division of Fisheries Research, Commonwealth Scientific and Industrial Research Organization, Cronula, Australia.

McGowan, M. F., and W. J. Richards. 1989. Bluefin tuna, *Thunnus thynnus*, larvae in the Gulf Stream off the southeastern United States: satellite and shipboard observations of their environment. U.S. National Marine Fisheries Service Fishery Bulletin 87:615–631.

Meekan, M. G., and L. Fortier. 1996. Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian Shelf. Marine Ecology Progress Series 137:25–37.

Nielsen, E., and K. Richardson. 1996. Can changes in the fisheries yield in the Kattegat (1950–1992) be linked to changes in primary production? ICES Journal of Marine Science 53:988–994.

Nixon, S. W. 1988. Physical energy inputs and the comparative ecology of lake and marine ecosystems. Limnology and Oceanography 33:1005–1025.

Olson, D. B., O. T. Brown, and S. R. Emmerson. 1983. Gulf Stream frontal statistics from Florida Straits to Cape Hatteras derived from satellite and historical data. Journal of Geophysical Research 88:4569–4577.

Paffenhöfer, G.-A. 1985. The abundance and distribution of zooplankton on the southeastern shelf of the United States. Pages 104–117 *in* Atkinson et al. (1985).

Pietrafesa, L. J. 1989. The Gulf Stream and wind events of the Carolina Capes shelf. National Undersea Research Program, National Oceanic and Atmospheric Administration, National Undersea Research Program Report 89-2, Wilmington, North Carolina.

Pietrafesa, L. J., G. S. Janowitz, and P. A. Wittman. 1985. Physical oceanographic processes in the Carolina Capes. Pages 23–32 *in* Atkinson et al. (1985).

Pomeroy, L. R. 1985. The microbial foodweb of the southeastern U.S. continental shelf. Pages 118–129 *in* Atkinson et al. (1985).

Powles, H., and B. W. Stender. 1976. Observations on composition, seasonality and distribution of ichthyoplankton from MARMAP cruises in the south Atlantic bight in 1973. South Carolina Marine Resources Center Technical Report, Series 11, South Carolina Wildlife and Marine Resources Department, Charleston.

Powell, A. B., and R. E. Robbins. 1994. Abundance and distributions of ichthyoplankton along an inshore-offshore transect in Onslow Bay, North Carolina. NOAA (National Oceanic and Atmospheric Administration) Technical. Report NMFS (National Marine Fisheries Service) 120, Washington, D.C.

Powell, A. B., and R. E. Robbins. 1998. Ichthyoplankton adjacent to live-bottom habitats in Onslow Bay, North Carolina. NOAA (National Oceanic and Atmospheric Administration) Technical Report. NMFS (National Marine Fisheries Service) 133, Washington, D.C.

Ryan, J. P., and J. A. Yoder. 1996. Long-term and event-related pigment distributions during the unstratified period in South Atlantic Bight outer margin and middle shelf waters. Continental Shelf Research 16:1165–1183.

Singer, J. J., L. P. Atkinson, J. O. Blanton, and J. A. Yoder. 1983. Cape Romain and the Charleston Bump: historical and recent hydrographic observations. Journal of Geophysical Research 88:4685–4697.

Turner, J. T. 1984. The feeding ecology of some zooplankters that are important prey items of larval fish. NOAA (National Oceanic and Atmospheric Administration), NMFS (National Marine Fisheries Service), Technical Report 7, Washington, D.C.

Vaughan, D., C. S. Manooch, III, and J. Potts. 2001. Assessment of the wreckfish fishery on the Blake Plateau. Pages 105–120 *in* G. Sedberry, editor. Island in the stream: oceanography and fisheries of the Charleston Bump. American Fisheries Society, Symposium 25, Bethesda, Maryland.

Verity, P. G., D. B. Craven, and S. S. Bishop. 1988. Seasonal studies of production and mortality of planktonic protists in the coastal waters of Georgia. EOS 69:1086.

Verity, P. G., and five coauthors. 1993a. Outer shelf processes. Pages 45–74 *in* D. W. Menzel, editor. Ocean processes: U.S. continental shelf: a summary of research conducted in the South Atlantic Bight under the auspices of the U.S. Department of Energy from 1977 to 1991. U.S. Department of Energy OSTI–11674, Oak Ridge, Tennessee.

Verity, P. G., and seven coauthors. 1993b. Composition, productivity and nutrient chemistry of a coastal ocean planktonic food web. Continental Shelf Research 13:741–776.

Victor, B. C. 1986. Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). Marine Biology 90:317–326.

Wellington, G. M., and B. C. Victor. 1989. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Marine Biology 101:557–567.

Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1979a. Results of Marmap otter trawl investigations in the South Atlantic Bight. I. Fall, 1973. Marine Resources Research Institute, South Carolina Wildlife and Marine Resources Department Technical Report 33, Charleston.

Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1979b. Results of Marmap otter trawl investigations in the South Atlantic Bight. II. Spring, 1974. Marine Resources Research Institute, South Carolina Wildlife and Marine Resources Department Technical Report 40, Charleston.

Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1979c. Results of Marmap otter trawl investigations in the South Atlantic Bight. III. Summer, 1974. Marine Resources Research Institute, South Carolina Wildlife and Marine Resources Department Technical Report 41, Charleston.

Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1979d. Results of Marmap otter trawl investigations in the South Atlantic Bight. IV. Winter-early spring, 1975. Marine Resources Research Institute, South Carolina Wildlife and Marine Resources Department Technical Report 44, Charleston.

Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1980. Results of Marmap otter trawl investigations in the South Atlantic Bight. V. Summer, 1975. Marine Resources Research Institute, South Carolina Wildlife and Marine Resources Department Technical Report 45, Charleston.

Yoder, J. A. 1985. Environmental control of phytoplankton production on the Southeastern U.S. Continental Shelf. Pages 93–103 *in* Atkinson et al. (1985).

Yoder, J. A. 1983. Statistical analysis of the distribution of fish eggs and larvae on the southeastern U.S. continental shelf with comments on oceanographic processes that may affect larval survival. Estuarine, Coastal and Shelf Science 17:637–650.